Continental Shelf Research 103 (2015) 70–78

Contents lists available at ScienceDirect

Continental Shelf Research

journal homepage: www.elsevier.com/locate/csr

Research papers

Bubble Transport Mechanism: Indications for a gas bubble-mediated inoculation of benthic methanotrophs into the water column

Oliver Schmale [a,*], Ira Leifer [b,c], Jens Schneider v. Deimling [d], Christian Stolle [a], Stefan Krause [d], Katrin Kießlich [a], Andreas Frahm [a], Tina Treude [d,1]

[a] *Leibniz Institute for Baltic Sea Research Warnemünde (IOW), Seestrasse 15, D-18119 Rostock, Germany*
[b] *University of California, Santa Barbara (UCSB), Santa Barbara, CA 93106, USA*
[c] *Bubbleology Research International, Solvang, CA 93463, USA*
[d] *GEOMAR Helmholtz Centre for Ocean Research Kiel, Wischhofstrasse 1-3, D-24148 Kiel, Germany*

ARTICLE INFO

Article history:
Received 28 August 2014
Received in revised form
24 April 2015
Accepted 25 April 2015
Available online 30 April 2015

Keywords:
Gas vent
Methane
Bentho-pelagic bubble transport
Methanotrophs

ABSTRACT

The importance of methanotrophic microorganisms in the sediment and water column for balancing marine methane budgets is well accepted. However, whether methanotrophic populations are distinct for benthic and pelagic environments or are the result of exchange processes between the two remains an area of active research. We conducted a field pilot study at the Rostocker Seep site (Coal Oil Point seep field, offshore California, USA) to test the hypothesis that bubble-mediated transport of methane-oxidizing microorganisms from the sediment into the water column is quantifiable. Measurements included dissolved methane concentration showed a strong influence of methane seepage on the water-column methane distribution with strongly elevated sea surface concentrations with respect to atmospheric equilibrium (saturation ratio ~17,000%).

Using Catalyzed Reporter Deposition Fluorescence In Situ Hybridization (CARD FISH) analysis, aerobic methane oxidizing bacteria (MOB) were detected in the sediment and the water column, whereas anaerobic methanotrophs (ANME-2) were detected exclusively in the sediment. Critical data for testing the hypothesis were collected using a novel bubble catcher that trapped naturally emanating seep gas bubbles and any attached particles approximately 15 cm above the seafloor. Bubble catcher experiments were carried out directly above a natural bubble seep vent and at a nearby reference site, for which an "engineered" nitrogen bubble vent without sediment contact was created. Our experiments indicate the existence of a "Bubble Transport Mechanism", which transports MOB from the sediment into the water column. In contrast, ANME-2 were not detected in the bubble catcher. The Bubble Transport Mechanism could have important implications for the connectivity between benthic and pelagic methanotrophic communities at methane seep sites.

1. Introduction

After water vapor and carbon dioxide (CO_2), methane is the most relevant greenhouse gas on earth, contributing about 20% to radiative forcing by well-mixed greenhouse gases on a century timescale (IPCC, 2013). Significant natural marine methane sources are mud volcanoes (Etiope and Klusman, 2002), hydrothermal systems (Schmale et al., 2012b), and cold hydrocarbon seeps (Judd and Hovland, 2007). Due to global warming, flooded permafrost (Shakhova et al., 2010) and submarine Arctic gas hydrates (Berndt et al., 2014; Westbrook et al., 2009) are currently under debate as additional drivers for increasing marine methane emissions to the atmosphere.

Due to their high organic matter content, continental slope and marginal sea sediments have huge methane generation potential by biogenic or thermogenic processes (Judd and Hovland, 2007; Reeburgh, 2007). In areas where methane is present in sediment pore fluids or in the water column, it serves as an important energy and carbon source for a complex microbial community (Knittel and Boetius, 2009; Valentine, 2011). Depending on the availability of methane and either oxygen or sulfate, microbial methane oxidation in the marine environment is conducted by aerobic methane-oxidizing bacteria (MOB) and anaerobic methanotrophic archaea (ANME), respectively. Although ANME activity is more relevant in the sediment, MOB represent the dominant microbial methane sink in the water column. MOB can be

---

[*] Corresponding author.
E-mail address: oliver.schmale@io-warnemuende.de (O. Schmale).

[1] Present address: University of California, Los Angeles, Department of Earth, Planetary & Space Sciences and Atmospheric & Oceanic Sciences, Los Angeles, CA 90095, USA.

http://dx.doi.org/10.1016/j.csr.2015.04.022
0278-4343/

subdivided into the three main groups, Type I, II and X (Hanson and Hanson, 1996). There are three phylogenetically distinct groups of ANME (ANME-1, 2, and 3), which are commonly associated with sulfate-reducing bacteria (Knittel et al., 2005). This so called “benthic methane filter” (Sommer et al., 2006) is very efficient and removes a major fraction of upward-migrating, dissolved methane in sediments by converting it into carbonates (Peckmann et al., 2001) and biomass (Nauhaus et al., 2007). In addition to sediment processes, the pelagic methane filter is dominated by MOB that decrease dissolved water column methane before it can enter the atmosphere (Reeburgh, 2007). In the water column, time-scales of microbial methane degradation below the wave-mixed layer are relatively short compared to ventilation to the atmosphere, preventing contribution from deep methane to atmospheric methane budgets (Rehder et al., 1999). However, methane bubbles largely bypass the benthic and pelagic microbial filter, enabling highly efficient transport of methane from the sediment towards the sea surface. Dissolution of bubbles rising from the seabed elevates methane concentrations in the overlying water column (McGinnis et al., 2006; Schmale et al., 2010). The vertical distribution of such dissolved methane from gas plumes and hence the potential for atmospheric impact depends on (a) water depth, (b) initial bubble size and gas fraction therein, (c) bubble dissolution kinetics, (d) local oceanographic conditions such as currents and density stratification (Leifer and Patro, 2002; Schmale et al., 2010), and (e) microbial methane oxidation (Valentine et al., 2001). Recent studies in the water column surrounding hydrocarbon seeps indicated an elevated abundance of methanotrophic microorganism in the near field of gas bubble plumes (Schubert et al., 2006). The enhanced methane concentration in the seep-affected water column stimulates the activity of methane oxidizers (Valentine et al., 2001) and might lead to a rise in the abundance of methane-oxidizing microbes in the aging plume water as was shown by Crespo-Medina et al. (2014) in the Deepwater Horizon plume and by de Angelis et al. (1993) in an aged hydrothermal plume.

Laboratory (Zhou and Mopper, 1998), modeling (Sadhal and Johnson, 1983), and field studies (Leifer and Clark, 2002) show that bubbles vertically transport surface-active substances (surfactants). Surfactants are compounds with hydrophobic and hydrophilic characteristics, which readily attach to gas/water interfaces (Schaefer et al., 1998; Wan and Wilson, 1994). To this group of substances belong colloidal, surface active particles which can consist of mineral particles (clay), organic macromolecules (proteins, lipids, and hydrocarbons), and even bacteria and viruses (Wan and Wilson, 1994).

Laboratory studies have shown that the accumulation of microorganisms on bubble surfaces facilitates their transport through a sandy matrix (Powelson and Mills, 1998; Wan et al., 1994). In contrast to studies regarding the transport of colloids on gas/water interfaces within groundwater environments (e.g., Powelson and Mills, 1998; Wan and Wilson, 1994; Wan et al., 1994), the relevance of this transport mechanism for the marine environment is discussed only rudimentarily in the literature (Leifer and Judd, 2002; Schubert et al., 2006). The accumulation of particles at the sea surface/atmosphere interface and the controlling mechanisms have long been the subject of different scientific investigations (e.g., Cunliffe et al., 2013; and references therein). In this interface, wind-driven surface-waves break and form bubble clouds. This well-studied mechanism sparges particles and surface active substances in the upper water column and transports them to the sea-surface microlayer (Bezdek and Carlucci, 1972; Wallace and Duce, 1978). This transport mechanism is hypothesized to influence microorganism abundance and microbial community diversity in the sea-surface microlayer (Cunliffe et al., 2013). Laboratory studies also show that bacterial enrichment at the sea-surface (the so-called bacterioneuston) affects air-sea gas exchange (Upstill-Goddard et al., 2003).

Studies at the sediment/water interface showed that resuspension (Shimeta et al., 2002) and submarine fluid discharge (Campbell et al., 2013) can transport microorganisms from the sediment into the water column and that these transport mechanisms have implications on the microbial community structure within the water column. Here, we hypothesize that a bubble-mediated transport mechanisms between the benthic and pelagic habitats represents an additional exchange process. More specifically, for an environment influenced by gas seepage, we hypothesize that gas bubbles transport methanotrophic microorganisms from the sediment into the water column, a process we termed the “Bubble Transport Mechanism”. This hypothesized mechanism would influence the water column methanotrophic community, thereby indirectly providing feedback mechanisms for dissolved methane concentrations in the water column with the potential to impact the sea/atmosphere methane flux. To test our bubble transport hypothesis we conducted a pilot field study at a natural gas bubble seepage area (informally named Rostocker Seep) in the Coal Oil Point seep field, offshore Southern California, USA. Key to this pilot study was the development of a bubble collection device (bubble catcher) that collected gas bubbles after they emerged from the seafloor together with any attached surfactant particles.

2. Material and methods

2.1. Study site

The Santa Barbara basin (California, USA) contains one of the world's largest and best investigated hydrocarbon seep fields, the Coal Oil Point seep field (Allen et al., 1970; Clark et al., 2003; Hornafius et al., 1999; Fig. 1). The seep field is located in water depths between a few meters and 80 m, extending from near the beach to 3 km offshore (Hornafius et al., 1999; Leifer et al., 2010). Seepage is concentrated above the Coal Oil Point and South Ellwood Anticlines, which harbors Miocene age oil in the Monterey Formation (Fischer, 1977).

A wide diversity of seepage has been documented in the Coal Oil Point seep field from sporadic single bubble vents releasing gentle bubble emanations to intense high-flow vents that span a broad range of bubble sizes, although generally radius $r > 1000$ μm (Leifer, 2010). Mean seep gas composition is 87.5% methane, 5.1% ethane, 3.1% propane and 1.3% carbon dioxide along with trace

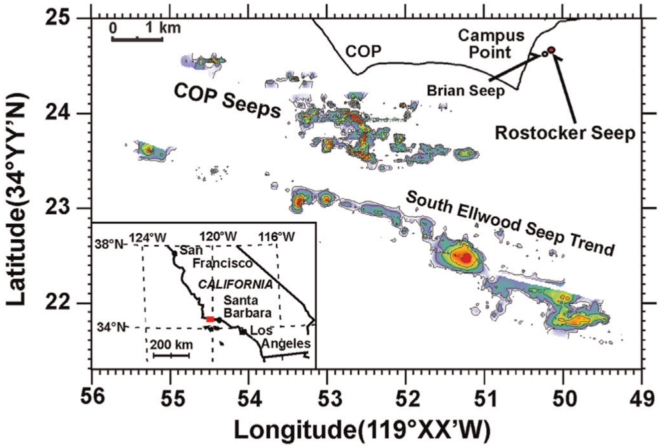

Fig. 1. Map of sonar-derived seepage activity in the Coal Oil Point (COP) seep field. Adapted from Leifer et al. (2010). Rostocker Seep (red dot) is at 34°24.230′N; 119°50.428′W.